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The type species of *Apiognomonia*, *A. veneta*, with its *Discula* anamorph is distinct from *A. errabunda*

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ABSTRACT

Species of *Apiognomonia* with their *Discula* anamorphic states in the Gnomoniaceae, Diaporthales, are known throughout the temperate Northern Hemisphere and cause diseases such as sycamore or plane tree anthracnose. The genus *Apiognomonia* was described based on *A. veneta* as the type species; however, there has been disagreement about whether or not *A. veneta* is a synonym of *A. errabunda*. Using morphological, ecological, and DNA sequence data we conclude that *A. errabunda* and *A. veneta* are different species, although very closely related; thus, *A. veneta* is the correct name for the type species of *Apiognomonia*. This conclusion is based on a combined analysis of sequences from the ITS regions of nuclear rDNA for 51 isolates from host plants of eight genera and intron regions from actin, calmodulin and translation elongation factor 1-alpha for over 25 isolates. The type species of the genus *Discula* is *D. nervisequa*, the earliest available epithet for *D. platani*, the lectotype of *Discula*. *D. nervisequa* is the anamorph of *A. veneta*. Based on an examination of the type specimen, we determined that the commonly used name for the anamorph of *A. errabunda*, *D. umbrinella*, refers to another species. *A. veneta* and *A. errabunda* including their anamorphs are described and illustrated. An account of all synonyms and excluded synonyms is presented.

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Introduction

Species of *Apiognomonia* with their *Discula* anamorphic states are known throughout the temperate Northern Hemisphere. Like most members of the Gnomoniaceae as defined by Castlebury et al. (2002), species of *Apiognomonia* produce minute perithecia on fallen, usually over-wintered, leaves. Conidial structures are produced on living leaves and young twigs while the inconspicuous teleomorph remains hidden in the leaf litter. *A. errabunda* and *A. veneta*, often reported as their *Discula* states, cause serious tree diseases such as anthracnose

diseases of *Cornus* (dogwood), *Fagus* (beech), *Fraxinus* (ash), *Platanus* (sycamore, plane), and *Quercus* (oak) in North America (Southworth 1889; Boewe et al. 1954; Neely & Himelick 1963, 1965; Hepting 1971; Sinclair et al. 1987; Hibben & Daughtrey 1988; Redlin 1991; Windham et al. 1994; Daughtrey et al. 1996; Zhang & Blackwell 2001) and Europe (Sempio 1933a, 1933b; Butin & Zycha 1973; Sinclair et al. 1987; Morelet 1989; Fell 1996; Tello et al. 2000). Plane tree anthracnose has also been reported from Australia (Milne & Hudson 1987), New Zealand (Brien 1939; Hitchcock & Cole 1978; Pennycook 1989), South Africa (Swart et al. 1990), and South America (Sinclair et al.

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1987). *A. errabunda*, often as its *Discula* anamorph, is reported as one of the most common endophytes in healthy *Fagus* and *Quercus* trees (Sieber & Hugentobler 1987; Danti et al. 2002).

The genus *Apiognomonia* is morphologically similar to *Gnomonia* in the lack of stromata and having solitary perithecia each with a central beak developing on leaves. Unlike *Gnomonia* having equally one-septate ascospores (Sogonov et al. 2005), *Apiognomonia* has been defined as having unequally two-celled ascospores (Müller & von Arx 1962; Barr 1978, 1991). In the original generic description, von Höhnel (1917) introduced the genus *Apiognomonia* for leaf-inhabiting fungi that lack a stroma and produce upright, beaked perithecia with hyaline, elongated to fusiform ascospores having two unequal cells. He stated that the ascospores were unequally one-septate without defining whether the upper or lower cell was larger. As a result Monod (1983) included species with a septum in either the upper or lower part of the ascospore, whereas Barr (1978) included only species with a septum in the lower portion of the ascospore.

Historically, there has been confusion about the correct names for the type and related species of both *Apiognomonia* and *Discula*. When von Höhnel (1917) established the genus *Apiognomonia*, he designated the type species as *A. veneta* based on *Laestadia veneta* Sacc. & Speg. 1878, a fungus on *Platanus* (Saccardo 1878), and did not mention any other species. In 1918, von Höhnel listed *Apiognomonia* with three additional species, *A. errabunda* (Rob.) Höhn., *A. erythrostoma* (Fr.) Höhn., and *A. inaequalis* (Auersw.) Höhn. Klebahn (1902) collected this species and sent it to Saccardo who considered Klebahn's collection to be *L. veneta*. However, Klebahn (1902) doubted the placement of this fungus in *Laestadia* and renamed the fungus *Gnomonia veneta* (Sacc. & Speg.) Kleb. Later Klebahn (1914) found this binomial already in use for another species, *Gnomonia veneta* Speg. (Spegazzini 1879) on *Ostrya carpinifolia*, and renamed the species based on *L. veneta* as *G. platani* Kleb.

The earliest description of a fungus now referred to as *Apiognomonia errabunda* (Roberge) Höhn. was by Roberge who observed a fungus on *Fagus sylvatica* and named it *Sphaeria errabunda* Roberge (in Desmazières 1848). Auerswald (1869) transferred this species to *Gnomonia* suggesting that it also occurs on *Quercus*. After studying the biology of the fungi from *Quercus*, Klebahn (1918) assigned the name *Gnomonia quercina* Kleb. stating that these fungi may also belong to the species *G. errabunda* (Roberge) Auersw. on *Fagus*. Although some authors have recognized *A. veneta* based on *Laestadia veneta* to be the type species of *Apiognomonia* (Barr 1978), others have considered *A. veneta* to be a synonym of *A. errabunda* (Boerema & Verhoeven 1972 as *Gnomonia*, Kobayashi 1970; Müller & von Arx 1962; von Arx 1951).

The anamorphic states of *Apiognomonia* have generally been recognized in *Discula* Sacc. 1884 on twigs, and *Gloeosporium* Desm. & Mont. 1856 on leaves. The link between these two, as well as their links to the teleomorph, was first discovered by Klebahn (1902, 1918). In the first paper, he also linked *Sporonema platani* Bäumler 1890, another anamorphic state occurring on fallen leaves of *Platanus* in winter and spring, to the other states. *Gloeosporium castagnei*, the type species of *Gloeosporium*, is now recognized in *Marssonina* as the anamorph of *Drepanopeziza* in the *Helotiales* (von Arx 1957, 1970). Therefore, the anamorphs of *Apiognomonia* have been placed in *Discula*.

The main objective of this paper is to determine whether *A. veneta* and *A. errabunda* are separate species or synonyms. Fresh isolates and herbarium specimens from a range of hosts were examined and characterized using DNA sequence data and morphological features. A second objective is to determine the correct names for the species of *Apiognomonia* and the type species of *Discula*. The earliest name to be applied is based on an examination of authentic and type specimens representing the numerous synonyms. Descriptions, illustrations, and DNA sequences for all taxa are provided.

Materials and methods

Preparation and morphological examination of specimens and cultures

Fresh material was collected in Canada (British Columbia), Russia (Novgorod, Nizhniy Novgorod, Tver' provinces), Switzerland (Geneve, Ticino, Vaud), and the USA (Maryland, Pennsylvania, Tennessee, Washington) in 2005–2006. Living and fallen leaves, and living, dead but still attached, and fallen twigs were examined for the presence of conidiomata and ascomata. Those containing fungal structures were air-dried and stored in paper bags or envelopes.

Herbarium specimens were obtained from the US National Fungus Collections (BPI) as well as the Museum Botanicum Berolinense (B), the Farlow Reference Library and Herbarium of Cryptogamic Botany in Harvard University (FH), the Royal Botanic Garden at Kew (K), the Leiden University branch (L) of the Nationaal Herbarium Nederland, the Musée et Jardins Botanique Cantonaux in Lausanne (LAU), the Botanische Staatssammlung München (M), and the New York State Museum Mycological Collections Herbarium (NYS).

Fresh and herbarium material was first observed on natural substrata using a Wild M5A (Wild Heerbrugg, Heerbrugg, Switzerland) or Leica MZ APO (Leica Microsystems, Weitzlar, Germany) dissecting microscope and photographed with a DXM 1200 digital camera (Nikon Instruments, Melville, NY). Perithecia and pycnidia-like conidiomata were extracted from leaf tissue with a sterile surgical scalpel under a dissecting microscope, placed into a drop of 3 % aqueous potassium hydroxide, 7 % aqueous sodium acetate solution or water on a clean microscope slide. After rehydration, perithecia were observed. Perithecia and pycnidia-like conidiomata were crushed to release their contents, which were transferred with an attenuated glass capillary or a scalpel to a clean area of the slide. For acervular conidiomata, a small part of the conidial mass with some underlying hyphal mat intermixed with leaf tissue was extracted to a slide. Examined material was covered with a cover slip and observed under differential interference contrast (DIC) illumination with an Axioplan2 microscope (Carl Zeiss, New York, NY) and photographed.

For the isolation of pure cultures, fresh material was rehydrated in 7 % sodium acetate solution or sterile water and crushed. Ascospores and ascii or conidia were removed by means of an attenuated glass capillary or a micropipette and transferred to corn meal agar (CMA; Sigma, St Louis, MO) plates containing 1 % (v/v) of an antibiotic solution (0.2 %

streptomycin sulphate and 0.2 % neomycin sulphate in sterile, distilled water). Plates were incubated at room temperature for 24 h. Germinated ascospores or conidia were transferred to fresh CMA or potato dextrose agar (PDA, Difco, Becton, Dickinson & Company, Sparks, MD) and incubated at room temperature. Cultures sequenced in this study were deposited at the Centraalbureau voor Schimmelcultures (CBS) in Utrecht, The Netherlands. For macroscopic descriptions of colonies, strains were grown on malt extract agar (MEA, Bacto, Becton, Dickinson, Sparks, MD). Cultures were placed in an incubator with a 12 h day/night cycle with blacklight (near uv) and cool white fluorescent light at 23 °C. Colours were determined according to Kornerup & Wanscher (1978).

Original software (Sogonov 2005) built on the base of MS Access 2000 (Microsoft Corporation, Bellevue, WA) was used for collecting and storing data and images of the samples and for making statistical measurements of the fungal structures. Measurements in descriptions are minimum/maximum values observed and range from first to third quartile. Arithmetic means, standard deviations, and number of measurements are given in parentheses. Thus, measurements are provided as (min-)Q₁-Q₃(-max) × (min-)Q₁-Q₃(-max) µm (mean ± s.d. × mean ± s.d. µm, n = x). Images were processed with Adobe Photoshop 5 (Adobe Systems, Inc., San Jose, CA).

DNA amplification and sequencing

Genomic DNA was extracted directly from actively growing surface mycelium scraped from PDA plates with the PUREGENE Cell and Tissue kit (Genta Systems, Minneapolis, MN) according to the manufacturer's instructions using approximately 50 mg fresh mycelium. For some collections, the ITS region was amplified directly from perithecial or conidiomatal contents in one of two ways. A small amount of ascus or conidial masses was extracted from a perithecium or conidioma with a sterile scalpel under the dissecting microscope and placed on the inner sidewall of a 0.2 ml PCR tube cap. Approximately 5 µl PCR-grade water were added to the mass of spores with a micropipette. Alternatively, a perithecium or conidioma was placed in a drop of PCR-grade water on a fresh microscope slide and squeezed using a scalpel. Then approximately 5 µl of the water containing a cloud of ascus or conidia was transferred either using a micropipette or a sterile glass capillary to the inner sidewall of a 0.2 ml PCR tube as above. PCR tubes containing spore suspensions were stored at -18 °C until amplification. The spore suspension was then spun to the bottom of the tube in a microcentrifuge (~30 s) after the PCR mix had been added to the tube. Before amplification, the spore suspensions were incubated for a further 5 min at 95 °C.

The ITS regions 1 and 2, including the 5.8S rDNA and intron regions in the actin, calmodulin and translation elongation factor 1-alpha (EF1-α) genes were amplified in 25 or 50 µL reactions on a GeneAmp 9700 thermal cycler (Applied Biosystems, Foster City, CA) using the following conditions: 0.2–0.3 ng µl⁻¹ genomic DNA, 4 pmol µl⁻¹ each dNTP, 0.05 units µl⁻¹ DNA polymerase (AmpliTaq®, Applied Biosystems, Foster City, CA or GeneChoice, Frederick, MD), 0.5 pmol µl⁻¹ each primer and 10 % vol. of the manufacturer's supplied 10× PCR buffer containing 15 mM magnesium chloride. The thermal

cycler programme was as follows: 2 min at 95 °C followed by 35 cycles of 30 s at 94 °C, 30 s at 55 °C, 1 min at 72 °C, with a final extension period of 10 min at 72 °C. If no amplicon was obtained from a reaction under these conditions, the annealing temperature was decreased to 50 or 52 °C and/or 4 % of DMSO (v/v) was added to the reaction mix. After amplification, the PCR products were purified with ExoSAP-IT (USB, Cleveland, OH) according to the manufacturer's instructions. ITS regions 1 and 2, including the 5.8S rDNA, were amplified and sequenced using the primers ITS5 and ITS4 (White et al. 1990). Intron regions of the actin, calmodulin, and EF1-α genes were amplified and sequenced using primers designed by Carbone & Kohn (1999).

Sequence alignment and analyses

Raw sequences were edited using Sequencher version 4.2 for Windows (Gene Codes Corporation, Ann Arbor, MI). Alignments were manually adjusted using BioEdit 7.0.5.2 (Hall, <http://www.mbio.ncsu.edu/BioEdit/>). Sequences are deposited in GenBank as DQ313524–DQ313643, DQ318034–DQ318036, and DQ994610–DQ994617 (Table 1). The alignment is deposited in TreeBASE with matrix accession number M2956. Trees were inferred by MP using the heuristic search option with the random addition sequence (1K replications), MULTREES on and the branch swapping (tree bisection–reconnection) option of PAUP 4.0b10 (Swofford 2002). All aligned positions were included in the analysis. All characters were unordered and given equal weight during the analysis. Gaps were treated as a fifth base in the parsimony analysis. Relative support for branches was estimated with 1K BS replications (Felsenstein 1985) with MULTREES and TBR on and ten random sequence additions for the MP BSs (Fig 3).

Results

The combined sequence alignment consisted of ITS1–5.8S–ITS2 (522 bp), EF1-α (362 bp), actin (227 bp), and calmodulin (476 bp) gene regions for 25 isolates of *Apiognomonia veneta* and *A. errabunda* and an isolate *Cryptodiaporthe hystrix* as an outgroup with 1587 total characters, excluding missing data at the ends of the gene regions. Of the 1587 positions, 15 were parsimony-informative (four in ITS1–5.8S–ITS2 partition excluding two gapped positions, six in EF1-α, two in actin, three in calmodulin), 1463 were constant (504 in ITS1–5.8S–ITS2, 312 in EF1-α, 210 in actin, 476 in calmodulin) and 109 were variable but not parsimony-informative (14 in ITS1–5.8S–ITS2, 44 in EF1-α, 15 in actin, 36 in calmodulin). A larger analysis of ITS data for ca 100 gnomoniaceous taxa was used to determine that *C. hystrix* was the most appropriate outgroup taxon (trees not shown, unpublished data). The partition homogeneity test as implemented in PAUP 4.0b10 indicated no significant conflict among the data partitions ($P = 1.00$).

Table 2 lists the nucleotide substitutions for all the positions where at least two samples differed from the others. The table contains information about all the samples for which at least one region was sequenced in this study, as well some sequences obtained from GenBank (<http://www.ncbi.nlm.nih.gov>).

Table 1 – Sequences obtained in this study

Species	State	Locality	Herbarium specimen ^{a,b}	Culture ^{a,b}	Host plant	Collector	Sequences			
							ITS	Calmodulin	Actin	EF1- α
<i>Cryptodiaporthe aesculi</i>	Teleomorph	USA: Wisconsin	BPI 840942	AR 3640	<i>Aesculus hippocastanum</i>	W. Jaklitsch	DQ313557	DQ313587	DQ313616	DQ313558
<i>C. hystrix</i>	Teleomorph	Switzerland	LAU n.n., CBS H-11343	CBS 911.79	<i>Acer pseudoplatanus</i>	M. Monod	DQ313549	DQ313588	DQ313617	DQ313559
<i>Apiognomonia veneta</i>	Teleomorph	Canada: British Columbia	BPI 872191	AR 4311 = CBS 120401	<i>Platanus occidentalis</i>	M.V. Sogonov	DQ994611	DQ994615		
<i>A. veneta</i>	Teleomorph	France	-	CBS 342.86	<i>P. orientalis</i>	H.A. van der Aa	DQ313531		DQ318035	DQ318036
<i>A. veneta</i>	Teleomorph	Germany	-	IMB 12479 = DSM 62551	<i>Platanus sp.</i>	H. Zycha	DQ313547	DQ313607	DQ313635	DQ313584
<i>A. veneta</i>	Teleomorph	New Zealand	-	ICMP 6201	<i>P. orientalis</i>	L.A. Hitchcock	DQ313538	DQ313608	DQ313636	DQ313580
<i>A. veneta</i>	Teleomorph	New Zealand	-	ICMP 6202	<i>P. orientalis</i>	L.A. Hitchcock	DQ313537		DQ313637	
<i>A. veneta</i>	Teleomorph	New Zealand	-	ICMP 6203	<i>P. orientalis</i>	L.A. Hitchcock	DQ313539	DQ313609	DQ313638	DQ313581
<i>A. veneta</i>	Teleomorph	Switzerland	LAU n.n., CBS H-8792	CBS 897.79	<i>P. orientalis</i>	M. Monod	DQ313532	DQ313606	DQ313639	DQ313575
<i>A. veneta</i>	Teleomorph	Switzerland	BPI 871946	AR 4181 = CBS 119035	<i>P. orientalis</i>	M.V. Sogonov	DQ313552	DQ313605	DQ313634	DQ313577
<i>A. veneta</i>	Teleomorph	Switzerland		AR 4184 = CBS 119033	<i>P. orientalis</i>	M.V. Sogonov	DQ313544			
<i>A. veneta</i>	Anamorph on living leaves	Switzerland	BPI 871953	AR 4180 = CBS 119036	<i>P. orientalis</i>	M.V. Sogonov	DQ313551	DQ313591	DQ313620	DQ313582
<i>A. veneta</i>	Anamorph on living leaves	Switzerland	BPI 871954	AR 4182 = CBS 119034	<i>P. orientalis</i>	M.V. Sogonov	DQ313543	DQ313592		DQ313578
<i>A. veneta</i>	Anamorph on living leaves	Switzerland	BPI 871955	AR 4187 = CBS 119032	<i>P. orientalis</i>	M.V. Sogonov	DQ313553	DQ313593	DQ313621	DQ313579
<i>A. veneta</i>	Anamorph on living leaves	USA: Maryland	BPI 871189	AR 4178 = CBS 119038	<i>P. occidentalis</i>	M.V. Sogonov	DQ313550 ^b	DQ313610	DQ313633	DQ313576
<i>A. veneta</i>	Anamorph on overwintered leaves	USA: Maryland	BPI 871949	AR 4192 = CBS 119029	<i>P. occidentalis</i>	M.V. Sogonov	DQ313533	DQ313598	DQ313627	DQ313573
<i>A. veneta</i>	Anamorph on overwintered leaves	USA: Maryland	BPI 871950	AR 4198	<i>P. occidentalis</i>	M.V. Sogonov	DQ313534	DQ313599	DQ313626	DQ313572
<i>A. veneta</i>	Anamorph on overwintered leaves	USA: Maryland	BPI 871951	AR 4199	<i>P. occidentalis</i>	M.V. Sogonov	DQ313535	DQ313600	DQ313628	DQ313574
<i>A. veneta</i>	Anamorph on overwintered leaves	USA: Maryland	BPI 871952	no culture	<i>P. occidentalis</i>	M.V. Sogonov	DQ313536			
<i>A. veneta</i>	Anamorph on overwintered leaves	USA: Tennessee	BPI 872190	AR 4310 = CBS 120398	<i>P. occidentalis</i>	M.V. Sogonov	DQ994610	DQ994614		
<i>A. veneta</i>	Not clearly indicated - most likely anamorph on living leaves	Germany	-	DSM 4997	<i>Tilia sp.</i>	H. Butin	DQ313546	DQ313614	DQ313643	DQ313583
<i>A. errabunda</i>	Teleomorph	Canada: British Columbia	BPI 872192	AR 4312 = CBS 120400	<i>Quercus sp.</i>	M.V. Sogonov	DQ994612	DQ994616	DQ994617	

<i>A. errabunda</i>	Teleomorph	Switzerland	LAU n.n.	CBS 776.79	<i>Chamerion angustifolium</i>	M. Monod	DQ313524	DQ313601	DQ313629	DQ313561
<i>A. errabunda</i>	Teleomorph	Switzerland	LAU n.n., CBS H-8788	CBS 775.79	<i>Fagus sylvatica</i>	M. Monod	DQ313526	DQ313604	DQ313632	DQ313562
<i>A. errabunda</i>	Teleomorph	Switzerland	BPI 871943	AR 4185	<i>F. sylvatica</i>	M. Monod & M.V. Sogonov	DQ313545	DQ313602	DQ313630	DQ313566
<i>A. errabunda</i>	Teleomorph	Switzerland	LAU n.n.	CBS 777.79	<i>Populus tremula</i>	M. Monod	DQ313527	DQ313611	DQ313640	DQ313560
<i>A. errabunda</i>	Teleomorph	Switzerland	LAU n.n., CBS H-8784	CBS 774.79	<i>Sorbus aria</i>	M. Monod	DQ313530	DQ313613	DQ313641	DQ313563
<i>A. errabunda</i>	Teleomorph	USA: Maryland	BPI 871941	no culture	<i>Quercus palustris</i>	M.V. Sogonov	DQ313529			
<i>A. errabunda</i>	Teleomorph	USA: Washington	BPI 872189	AR 4293 = CBS 120404	<i>Rhus glabra</i>	M.V. Sogonov	DQ994613			
<i>A. errabunda</i>	Not clearly indicated - most likely teleomorph	Switzerland	-	AR 2813 = CBS 109747	<i>F. sylvatica</i>	M. Monod	DQ313525	DQ313603	DQ313631	DQ313565
<i>A. errabunda</i>	Anamorph on living leaves	Russia: Nizhniy Novgorod prov.	BPI 871959	AR 4218	<i>T. cordata</i>	M.V. Sogonov	DQ313554	DQ313594	DQ313623	DQ313567
<i>A. errabunda</i>	Anamorph on living leaves	Russia: Novgorod prov.	BPI 871960	AR 4223 = CBS 119191	<i>T. cordata</i>	M.V. Sogonov	DQ313555	DQ313596	DQ313625	DQ313571
<i>A. errabunda</i>	Anamorph on living leaves	Russia: Novgorod prov.	BPI 871961	AR 4219 = CBS 119031	<i>T. cordata</i>	M.V. Sogonov	DQ313556	DQ313595	DQ313624	DQ313585
<i>A. errabunda</i>	Anamorph on living leaves	Switzerland	BPI 871958	AR 4179 = CBS 119037	<i>T. cordata</i>	M. Monod	DQ313542	DQ313597	DQ313622	DQ313569
<i>A. errabunda</i>	Not clearly indicated - most likely anamorph on living leaves	Germany	-	DSM 4990	<i>Quercus</i> sp.	H. Butin	DQ313548	DQ313615	DQ313642	DQ313568
<i>A. errabunda</i>	Not clearly indicated - most likely anamorph on living leaves	USA: Wisconsin	-	ATCC 38312	<i>Q. alba</i>	D. Neeley	DQ313528	DQ313612	DQ318034	DQ313564
<i>A. errabunda</i>	Endophytic isolate	Switzerland	-	ZT 94154	<i>Castanea sativa</i>	G. Horat	DQ313541	DQ313589	DQ313618	DQ313570
<i>A. errabunda</i>	Endophytic isolate	Switzerland	-	ZT 94147	<i>Q. uercus robur</i>	G. Horat	DQ313540	DQ313590	DQ313619	DQ313586

a BPI = US National Fungus Collections, Beltsville, MD, USA; LAU = Musée et Jardins Botanique Cantonaux in Lausanne, Switzerland; CBS = Centraalbureau voor Schimmelcultures, Utrecht, the Netherlands; AR = Amy Rossman, third author; IMB = Institut für Mykologie, BBA, Berlin-Dahlem, Germany; DSM = Deutsche Sammlung von Mikroorganismen und Zellkulturen GmbH, Braunschweig, Germany; ICMP = International Collection of Microorganisms from Plants, Auckland, New Zealand; ATCC = American Type Culture Collection, Manassas, VA, USA; ZT = ETH Culture Collection, Zurich, Switzerland.

b A large part of the sequence is missing.

Table 2 – Polymorphic nucleotide sites among 50 isolates in the four studied genes in *Apiognomonia veneta* species complex

Species	Isolate numbers ^a	Host family	Geographic region ^b	ITS1-5.8S-ITS2					Calmodulin			Actin		EF1- α						
				44	117	142	182	183	477	37	166	169	58	163	110	216	275	286	302	333
<i>A. veneta/D. nervisequa</i>	CBS 897.79	Platanaceae	W.Eur.	C	G	C	A	-	C	C	A	C	T	A	C	G	T	G	A	C
	CBS 119035		W.Eur.	A	G
	CBS 119033		W.Eur.	/	/	/	/	/	/	/	/	/	/	/
	CBS 119036		W.Eur.	.	.	.	A	G
	CBS 119034		W.Eur.	/	/	/	/	/	/	/	/	/	/	/
	CBS 119032		W.Eur.	.	.	.	A	G
	DSMZ 62551		W.Eur.	T
	CBS 342.86		W.Eur.	/	/	/	/	/	/	/	/	/	/	/
	CBS 119038		E.N.Am.	.	.	.	N	G
	CBS 119029		E.N.Am.
	BPI 871950		E.N.Am.
	BPI 871951		E.N.Am.
	BPI 871952		E.N.Am.	/	/	/	/	/	/	/	/	/	/	/
	BPI 872190		E.N.Am.
	BPI 872191		W.N.Am.
	ICMP 6201		N.Zea.	T
	ICMP 6202		N.Zea.	/	/	/	/	/	/	/	/	/	/	/
	ICMP 6203		N.Zea.	T
	DSMZ 4997	Malvaceae	W.Eur.
<i>A. errabunda/D. tiliiae</i>	DSMZ 4990	Fagaceae	W.Eur.	.	.	.	-	.	G	T	G	A	A	G	G	A	C	T	G	T
	AJ293872		W.Eur.	.	.	.	-	.	G	/	/	/	/	/	/	/	/	/	/	/
	AJ293873		W.Eur.	.	.	.	-	.	G	/	/	/	/	/	/	/	/	/	/	/
	AJ293874		W.Eur.	.	.	.	-	.	G	/	/	/	/	/	/	/	/	/	/	/
	AJ293875		W.Eur.	.	.	.	-	.	G	/	/	/	/	/	/	/	/	/	/	/
	CBS 369.97		W.Eur.	.	.	.	-	.	G	/	/	/	/	/	/	/	/	/	/	/
	CBS 115298		W.Eur.	.	A	.	-	.	G	/	/	/	/	/	/	/	/	/	/	/
	CBS 115015		W.Eur.	.	A	.	-	.	G	/	/	/	/	/	/	/	/	/	/	/
	CBS 115919		W.Eur.	.	.	.	-	.	G	/	/	/	/	/	/	/	/	/	/	/
	CBS 115931		W.Eur.	.	.	.	-	.	G	/	/	/	/	/	/	/	/	/	/	/
	CBS 115969		W.Eur.	.	.	.	-	.	G	/	/	/	/	/	/	/	/	/	/	/
	CBS 115929		W.Eur.	.	.	G	-	.	G	/	/	/	/	/	/	/	/	/	/	/
	CBS 115008		W.Eur.	.	.	.	-	.	G	/	/	/	/	/	/	/	/	/	/	/
	CBS 115010		W.Eur.	.	.	.	-	.	G	/	/	/	/	/	/	/	/	/	/	/
	CBS 115017		W.Eur.	.	.	.	-	.	G	/	/	/	/	/	/	/	/	/	/	/
	CBS 115106		W.Eur.	.	.	.	-	.	G	/	/	/	/	/	/	/	/	/	/	/
	ATCC 38312		C.N.Am.	.	.	.	-	.	G	T	G	.	.	G	G	A	.	T	G	T
	BPI 871941		E.N.Am.	.	.	.	-	.	G	/	/	/	/	/	/	/	/	/	/	/
	BPI 872192		W.N.Am.	N	.	.	-	.	G	T	G	A	.	G	/	/	/	/	/	/
	CBS 109747		W.Eur.	.	.	.	-	.	G	T	G	.	.	G	G	A	.	T	.	T
	CBS 775.79		W.Eur.	.	.	.	-	.	G	N	G	.	.	G	G	A	.	T	.	T
	BPI 871943		W.Eur.	.	.	.	-	.	G	T	G	.	.	G	G	A	.	T	.	T
	ZT 94147		W.Eur.	.	.	.	-	.	G	T	G	.	.	G	G	A	.	T	.	T
	ZT 94154		W.Eur.	.	.	.	-	.	G	T	G	.	N	G	G	A	.	T	G	T
<i>BPI 871959</i>	BPI 871960	Malvaceae	E.Eur.	.	.	G	-	.	G	T	G	A	A	G	G	A	C	T	G	T
	CBS 119031		E.Eur.	.	.	G	-	.	G	T	G	A	A	G	G	A	C	T	G	T
	CBS 119037		W.Eur.	.	.	G	-	.	G	T	G	A	A	G	G	A	C	T	G	T
	CBS 774.79		W.Eur.	.	.	.	-	.	G	/	/	/	/	/	/	/	/	/	/	/
<i>BPI 872189</i>	BPI 872189	Miscellaneous	W.N.Am.	N	.	.	-	.	G	T	G	.	.	G	G	A	.	T	.	T
	CBS 777.79		W.Eur.	.	.	.	-	.	G	T	G	.	.	G	G	A	.	T	.	T
	CBS 776.79		W.Eur.	.	.	.	-	.	G	T	G	.	.	G	G	A	.	T	.	T

Sites with autapomorphies are not shown. Dots indicate identity with the first sequence. Hatched areas indicate unsequenced regions.

a Culture collection numbers are given for specimens that have living cultures available. For sequences obtained via direct PCRs or from living cultures lost before being deposited, herbarium (BPI) numbers are given. Numbers for sequences obtained from GenBank are indicated in italic. For four GenBank sequences with no information on their sample voucher numbers, the GenBank accession numbers are given.

b Abbreviations: W.Eur., Western Europe (France, Germany, the Netherlands, Switzerland); E.Eur., Eastern Europe (Nizhniy Novgorod, Novgorod, Tver oblasts in Russia); W.N.Am., Western North America (British Columbia in Canada and Washington in the USA); C.N.Am., Central North America (Wisconsin in the USA); E.N.Am., Eastern North America (Maryland, Pennsylvania, Tennessee in the USA); N.Zea., New Zealand.

Hatched areas indicate unsequenced gene regions. The combined dataset of four genes contains 17 positions with substitutions or insertion/deletion (indel) events in two or more isolates. Of these substitutions, seven can be used to distinguish two species corresponding to *A. veneta* and *A. errabunda*. Of the six positions in the ITS regions, one indel distinguishes the two species. Within the calmodulin and actin gene regions, one position each distinguishes the two species. Within the EF1- α region, there are six positions that differ, three of which distinguish the two species.

MP phylogenetic analysis of the combined alignment resulted in 12 equally parsimonious trees (length = 125, CI = 1.000, RI = 1.000, RC = 1.000), three of which contain a non-*Platanus* group as a separate clade (trees not shown) while in the others, non-*Platanus* isolates formed paraphyletic assembly at the base of the *Platanus* group. Individual actin (<70 % BS support), calmodulin (79 %), and EF1- α (98 %) gene trees all resolved a clade corresponding to *A. veneta* with non-*Platanus* isolates paraphyletic and basal to *A. veneta* (trees not shown). The ITS gene tree did not resolve either species. Fig 3 shows one randomly chosen MP tree generated for the combined alignment, with MP BS supports at branches. Only BS values 70 % or greater are shown. One clade with 100 % BS support included predominantly isolates from *Platanus* and is regarded as *Apiognomonia veneta*. A second group of isolates regarded as *A. errabunda* includes one clade of isolates predominantly from *Tilia* (93 %) and the remaining isolates from *Fagaceae* and some occasional hosts such as *Chamerion*, *Populus*, and *Sorbus*.

Taxonomy

***Apiognomonia veneta* (Sacc. & Speg.) Höhn., Ber. Deutsch. Bot. Ges. 35: 637 (1917).** *(Fig 1A–S)*

Basionym: *Laestadia veneta* (Speg.) Sacc. & Speg., Michelia 1: 351 (1878).

Apiospora veneta (Sacc. & Speg.) Kleb., Z. Pflanzenk. 7: 258 (1902).

Gnomonia platani Kleb., Verhandl. Deutsch. Bot. Ges. 1: 28 (1914).

[*Gnomonia veneta* (Sacc. & Speg.) Kleb., Jahrb. Wiss. Bot. 41: 533 (1905) non Speg., 1879.]

Type: Italy: Padova, in foliis *Platani occidentalis* dejectis, Feb. 1878, C. Spegazzini, Mycotheca Veneta 1266 (BPI 597949 – *lectotypus hic designatus*). — Switzerland: Geneva, park along Le Rhône river, *Platanus orientalis*, 22 May 2005, M. V. Sogonov MS0194 (BPI 871947, derived culture CBS 119033 = AR 4184 – *epitypus hic designatus*).

Anamorph

***Discula nervisequa* (Fuckel) M. Morelet, Bull. Soc. Sci. nat. d'Arch. Toulon Var. 203: 12 (1973).**

Basionym: *Fusarium nervisequum* Fuckel, Jahrb. nass. Ver. Naturk. 23/24: 369 (1870).

Gloeosporium nervisequum (Fuckel) Sacc., Michelia 2: 381 (1884).

Types: Germany: living and freshly fallen leaves of *Platanus orientalis*, summer, L. Fuckel?, Fungi Rhenani 427 (BPI bound – *lectotypus hic designatus*). — Switzerland: Geneva, Place de Charmilles, trees in a city street, *Platanus orientalis*, 31 May 2005, M. V. Sogonov MS0190 (BPI 871953, derived culture AR 4180 = CBS 119036 – *epitypus hic designatus*).

Hymenula platani Lév., Ann. Sci. nat. Bot., sér. 3 9: 128 (1848).
Fusarium platani (Lév.) Mont., Ann. Sci. nat. Bot., sér. 3 11: 55 (1849).

Gloeosporidium platani (Lév.) Höhn., Sber. Akad. Wiss. Wien, Math.-naturw. Kl., Abt. 1 125: 95 (1916).

[*Myxosporina platani* (Lév.) Höhn., Hedwigia 62: 48 (1921) non Ellis & Everh., 1894].

Type: France: “Gallia meridionali. Legit. cl. Castagne ad folia Platani orientalis”. Not seen.

Gloeosporium platani Oudem., Nederlandisch kruidkundig Archief, ser. 2 1: 258 (1873).

Type: The Netherlands: Zuidhoek near Naaldwijk, on leaves of *Platanus occidentalis*, 1872, L. D. van der Trappen, table 10, figure 16 (reprint at BPI: isotype as drawing).

Discella platani Oudem., Nederl. kruidkund. Arch., ser. 2 3: 150 (1877).

Type: The Netherlands: Amsterdam, twig of *Platanus orientalis*, Jan. 1877, C.A.J.A. Oudemans, Fungi Neerlandici Exsiccati 194 (B 700010442 ex Mycotheca Saccardiana – *lectotypus hic designatus*).

Gloeosporium nervisequum Fuckel **valsoideum* Sacc. Michelia 2: 381 (1881).

Gloeosporium valsoideum (Sacc.) Sacc., Sylloge Fungorum III: 716 (1884).

Type: Italy: Horto Patavino, in ramulis junioribus *Platani occidentalis*, Feb. 1881, G. Bizzozero (P.A. Saccardo, Fungi Italici, Illustr. 1048 – isotype as drawing)

Discula platani (Peck) Sacc., Syll. Fung. 3: 674 (1884).

[*Discella platani* Peck, N.Y. State Mus. Rep. 29: 49 (1878). non Oudem. 1877.]

Type: USA: New York: Bethlehem, twigs of *Platanus occidentalis*, May, year unknown, C.H. Peck (NYS – *lectotypus hic designatus*).

Myxosporium platani Ellis & Everh., Proc. Acad. nat. sci. Phil. 372 (1894).

Type: USA: West Virginia: Fayette, Nuttallburg, on dead limbs of *Platanus*, Apr. 1894, L. W. Nuttall 467, North American Fungi 3180 (BPI bound – *lectotypus hic designatus*).

Sporonema platani Bäumler, Öst bot Zeit 40: 17–19 (1890).

Placosphaeria platani (Bäumler) Limber, Mycologia 47: 398 (1955).

Type: Slovak Republic: near Bratislava, Aupark, ‘in pagina inferiore foliorum emortuorum *Platani occidentalis*’, Jan. 1888, J.A. Bäumler 989 (BPI 393077 – *lectotypus hic designatus*)

Fusicoccum veronense C. Massal., Bull. della Società bot. ital.: 255 (1900).

Type: ‘sui picciuoli marcescenti della foglie de *Platanus orientalis*, presso Verona; Marzo-Aprile 1900’. Not seen.

Perithecia hypophylloides, scattered irregularly over leaf blade, usually not numerous, immersed, black, becoming dark

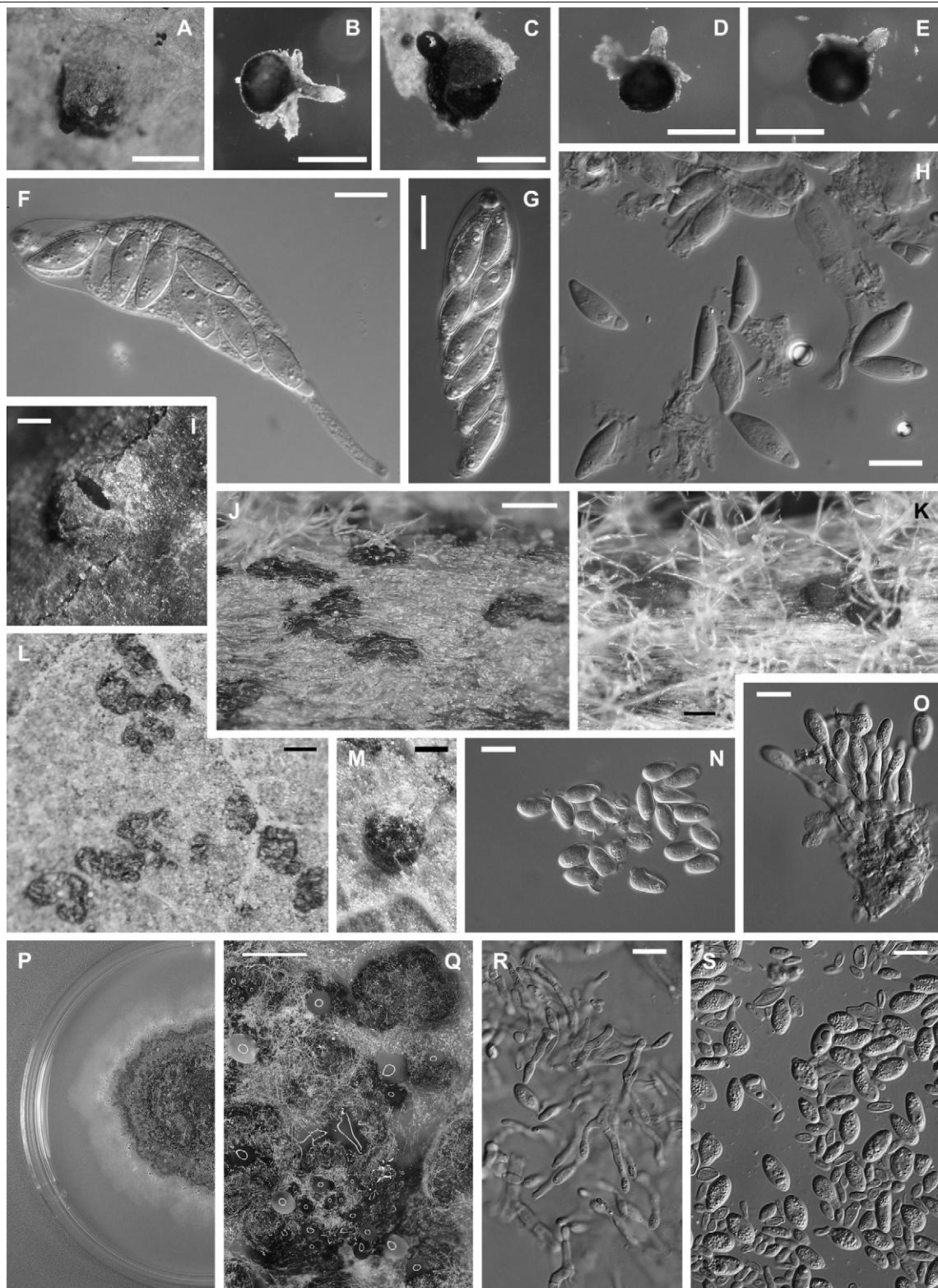


Fig 1 – *Apiognomonia veneta* teleomorph and anamorph states. (A) Perithecium on a leaf. (B–E) Extracted and rehydrated perithecia showing variability in length and placement of beak. (F, G) Ascospores. (H) Ascospores. (I) Acervula on a twig. (J, K) Acervulae on leaves. (L, M) Pycnidia-like conidiomata on an overwintered leaves. (N) Conidia from acervulae on twigs. (O) Conidiophores and conidia from acervulae on twigs. (P) Colony on PDA after 12 d of cultivation. (Q) Pycnidia-like conidiomata in colony on PDA after 17 d of cultivation. (R, S) Conidiophores and conidia from colonies on PDA after 15 d of cultivation. Specimen (culture) numbers: (A, C) Monod 441. (B, F, R, S) BPI 871947 (CBS 119033). (D, E, G) BPI 871189 (CBS 119038). (H) BPI 597950. (I) BPI 611704. (J) BPI 871953 (CBS 119036). (K) BPI 871955 (CBS 119035). (L) BPI 871950. (M) BPI 393080. (N) BPI 611748A. (O) North American Fungi 3180. (P, Q) BPI 871946 (CBS 119035). Host plants: (A–D, F, J, K, M, P–S) *Platanus orientalis*. (E, G–I, L–O) *P. occidentalis*. Bars: (A–E, I–M) = 200 µm, (F–H, N, O, R, S) = 10 µm, (Q) = 1 mm.

brown or black when moist, oblate to globose, (149–171–213(–274) μm high \times (152–202–284(–362) μm diam (mean = 200 \times 245, s.d. 33.3, n_1 = 37, n_2 = 44), collapsing cupulate from bottom or occasionally from side when dry. Beaks central, straight, black at base becoming pale at apex, length (57–88–138(–194) μm (mean = 112, s.d. 35.8, n = 31), basal diam (42–)52.5–73(–92.8) μm (mean = 62, s.d. 13.4, n = 31), distal diam (36–)49.5–68(–111) μm (mean = 60.8, s.d. 17.1, n = 31). Ascii clavate, length \times width (47–)56.5–73(–87) \times (12.5–)13–16(–19.5) μm (mean = 64.4 \times 14.3, s.d. 11.5, 1.7, n_1 = 21, n_2 = 21), with eight ascospores arranged irregularly fasciculate or, sometimes in lower part of ascus, obliquely in one longitudinal row, apical ring 3.5–5 μm diam. Ascospores fusiform, inequilateral (13–)15.5–17.5(–23) \times (3.5–)5–5.5(–7.5) μm (mean = 16.6 \times 5.3, s.d. 1.4, 0.6, n_1 = 181, n_2 = 180), l:b (2.5–)3–3.5(–4.5) (mean = 3.2, s.d. 0.3, n = 180), two-celled with a septum at (7.5–)17.5–21.5(–29.5) % (mean = 19.6, s.d. 3, n = 180) of ascospore length from basal end, ascospore ends blunt, rounded, lipid guttules usually absent or numerous but small (0.5–1 μm diam), appendages absent.

Conidiomata on twigs acervular, developing between cork and cortex, forming bumps ca 1 mm diam, that crack with age near apex, conidiogenous layer covering all the inner surface of acervular chambers. Conidiomata on veins and blades of living leaves acervular, irregularly round or oval ca 150–300 μm diam, initially developing under epidermis, flat, yellowish-brown, then breaking through epidermis and finally forming thick amorphous conidial masses above leaf surface. Conidiomata on veins and blades of over-wintered leaves superficial, non-ostiolate pycnidial, oblate to globose, ca 100–500 \times 100–350 μm , black, thick-walled, with one chamber containing whitish conidial mass. Conidiophores densely branched, length ca 30–50 μm . Conidiogenous cells usually phialidic, rarely with a few annellidic scars, irregular in shape, lageniform to cylindrical, gradually tapering to ends for one-quarter to three-quarters of their length, or abruptly narrowing to long neck at about half of the phialide length, or abruptly narrowing at apex, straight or curved, sometimes asymmetric swollen nodes, proliferating into other conidiogenous cells at basal or middle part, (10–)12.5–15.5(–23) \times (3–)3.5–5(–6.5) μm (mean = 14.3 \times 4.4, s.d. 2.7, 0.7, n_1 = 67, n_2 = 67), l:b (1.5–)2.5–4(–5.5) μm (mean = 3.4, s.d. 0.9, n = 67). Conidia broadly ellipsoid to oval, sometimes obovoid, often allantoid, occasionally curved or sinuate to slightly angular (7.5–)10.5–12.5(–15.5) \times (3.5–)5–6(–75) μm (mean = 11.5 \times 5.5, s.d. 1.2, 0.6, n_1 = 913, n_2 = 913), l:b (1–)1.5–2.5(–3.5) (mean = 2.1, s.d. 0.3, n = 913).

Colonies after 21 d at 20 °C in day/night illumination. PDA: 60–65 mm diam, densely cottony, plane, with rings of orange grey (6B2), brownish orange (6C3) to dark brown (6F4); reverse dark brown (6F4) with some pale spots in the outer part. MEA: 60–85 mm diam, velutinous with tufts in centre, then cottony, glabrous at margins, or cottony all-over, whitish; reverse colourless to brownish-orange (Sahara). On both media, freshly isolated cultures produce numerous black non-ostiolate pycnidia-like conidiomata 0.2–1 mm diam, breaking out discharging conidia in slimy drops.

Hosts: *Platanus* spp., isolated once from *Tilia*.

Geographical distribution: Mainly in temperate regions throughout the northern hemisphere, also from cultivated *Platanus* in

southern hemisphere, including Argentina (Milne & Hudson 1987), Australia (*ibidem*), Austria, Canada (British Columbia), Chile, Czech Republic, France, Germany, Hungary, Italy, Netherlands, New Zealand, Poland, South Africa (Swart et al. 1990), Switzerland, USA (California, Connecticut, Delaware, District of Columbia, Iowa, Maryland, Massachusetts, Michigan, New Jersey, New York, Pennsylvania, Ohio, Tennessee, Washington, West Virginia, Wisconsin).

Additional specimens examined:

Teleomorph: **Austria:** Vienna, Huetteldorf, *Platanus* sp., Mar. 1919, J. Weese (BPI 611694). — **Canada:** British Columbia: Vancouver, University of British Columbia campus, *P. orientalis*, 11 May 2006, M.V. Sogonov MS0395 (BPI 872191, derived culture CBS 120401 = AR 4311). — **Germany:** Hamburg, botanical garden, *P. orientalis*, 15 Apr. 1910, H. Klebahn (Jaap, Fungi Selecti Exsiccati 471b, BPI bound); Hamburg, botanic garden, *P. orientalis*, 1 Jul. 1910, Klebahn H. (Jaap, Fungi Selecti Exsiccati 471b, BPI 611763); Mecklenburg, between Schwerin & Zippendorf, *P. acerifolia*, 29 Apr. 1936, H. Sydow (BPI 611700). — **Poland:** Gorzów Wielkopolski region, Witnica municipality, Dąbroszyn (at the time of the collection Germany: Brandenburg), Tamsel, *P. acerifolia*, 20 Apr. 1935, P. Vogel (BPI 611699). — **Switzerland:** Geneva, park along Le Rhône river, *P. orientalis*, 22 May 2005, M. V. Sogonov MS0194 (BPI 871947, derived culture CBS 119033 = AR 4184); Vaud, campground Rolle, *P. orientalis*, 14 May 1976, M. Monod 57 (LAU); Vaud, Servion, *P. orientalis*, 26 May 1976, M. Monod 75 (LAU); Vaud, Montagny, *P. orientalis*, 22 Apr. 1977, M. Monod 215 (LAU, derived culture CBS 898.79); Vaud, Villeneuve (lake side), *P. orientalis*, 8 May 1878, M. Monod 429 (LAU, derived culture CBS 897.79); Vaud, Genolier (oak forest), *P. orientalis*, 16 May 1978, M. Monod 441 (LAU, derived culture CBS 899.79); Vaud, Lausanne, Parc Bourge, *P. orientalis*, 24 May 2005, M.V. Sogonov MS0191 (BPI 871946, derived culture CBS 119035 = AR 4181); Ticino, Paradiso, *P. orientalis*, 28 May 2005, M. V. Sogonov MS0210 (BPI 871948). — **USA:** Maryland: Prince George's Co., Beltsville, forest near the parking place near the Building 011A, mixed forest, *P. occidentalis*, 7 Apr. 2005, M. V. Sogonov MS0168 (BPI 871944A); *ibidem*, *P. occidentalis*, 8 Apr. 2005, M. V. Sogonov MS0182 (BPI 871945); Prince George's Co., College Park, Anacostia River Park, hardwood forest, *P. occidentalis*, 7 May 2005, M. V. Sogonov MS0188 (derived culture CBS 119038 = AR 4178). New York: Ithaca, *P. occidentalis*, 17 May 1907, C.W. Edgerton (BPI 611754); *ibidem*, University campus, *P. occidentalis*, 30 Apr. 1919, C.E. Chardon (BPI 611705). Pennsylvania: Franklin Co., Cove Gap, Buchanan Birthplace State Park, *P. acerifolia*, 5 May 2006, M. V. Sogonov MS0357 (BPI 872110). West Virginia: Fayette Co., river bank, *P. occidentalis*, 14 Mar. 1896, L.W. Nuttall 838 (BPI 597950, BPI 597951).

Anamorph on twig: **The Netherlands:** Amsterdam, *P. orientalis*, Jan. 1877, C. A. J. A. Oudemans, Fungi Neerlandici Exsiccati 194 [B 700010442 – lectotype of *Discella platani* Oudem., B 700010441 – isotype]; Amsterdam, *P. sp.*, Jan. 1897, C. A. J. A. Oudemans, Fungi Neerlandici Exsiccati 1293 [L 0194367, 0194370]; *P. sp.*, [date unknown], C. A. J. A. Oudemans, Fungi Neerlandici Exsiccati s.n. [L 0194369] — **USA:** Connecticut: Clinton, *P. occidentalis*, 20 Jun. 1924, Humphrey (BPI 611751); District of Columbia: *P. occidentalis*, 17 May 1925, J.S. Boyce (BPI 611728). Maryland: Prince George's Co., USDA ARS, Beltsville, near B011A, *P. occidentalis*, 5 Jul. 2005, M.V. Sogonov MS0211a (BPI 871957). Michigan: Ann Arbor, *P. occidentalis*, 17 Jul. 1924, V. Dow Baxter (BPI 611743). New York: Bethlehem, *P. occidentalis*, May (year unknown), C. H. Peck [NYS, lectotype of *Discella platani* Peck 1978 non *Discella platani* Oudem. 1877]; Long Island, Nassau Co., Glen Cove, *P. occidentalis*, 7 Jun. 1910, R. Marshall (BPI 611748A); Staten Island, *P. occidentalis*, 1910, (collector unknown) (BPI 611738); Dutchess Co., Tivoli, *P. occidentalis*, Jun. 1924, I.L. Neddmond (BPI 611753); West New Brighton, *P. occidentalis*, 3 Jun. 1910, F.C. Boes (BPI 611727). West Virginia: Morgantown, *P. occidentalis*, 23 May 1912, (collector unknown) (BPI 611805); Morgantown, campus, *P. occidentalis*, 28 Jun. 1919, J. L. Sheldon (BPI 611704).

Anamorph on living leaves: France: vicinity of Marseille, *P. occidentalis*, before 1848, M. Castagne? [Desmazières, Plantes Cryptogames de France, edit. 1, 1749 (BPI bound) — possibly the type of *Discula nervisequa*] — Germany: Bavaria, Bayreuth, *P. orientalis*, Aug. 1875, F. Thümen [Thümen, Mycotheca Universalis 1279 (BPI bound)]; *ibidem*, *P. orientalis*, Spring 1875, F. Thümen [Thümen, Mycotheca Universalis 481a (BPI bound)]; Hamburg, botanical garden, *P. orientalis*, 1 Jul. 1910, H. Klebahn [Jaap, Fungi Selecti Exsiccati 471a (BPI bound)]; Hamburg, Botanic Garden, *P. orientalis*, 15 Apr. 1910, Klebahn H. (BPI 611762) — Switzerland: Ticino, Paradiso, *P. orientalis*, 28 May 2005, M. V. Sogonov MS0203 (BPI 871955, derived culture CBS 119032 = AR 4187); Vaud, Lausanne, Parc Bourge, *P. orientalis*, 24 May 2005, M. V. Sogonov MS0192 (BPI 871954, derived culture CBS 119034 = AR 4182). — USA: California: *P. racemosa*, (date unknown), H. W. Harkness [North American Fungi 1630 (BPI bound)]; Connecticut: New Haven, *P. occidentalis*, Spring 1916, P. Spaulding (BPI 611709); *ibidem*, 28 May 1935, J. R. Hansbrough (BPI 611707); Delaware: Newark, *P. occidentalis*, 10 May 1910, C. L. Shear (BPI 611710); *ibidem*, 20 Jun. 1907, H. S. Jackson 1870 (BPI 611712); District of Columbia: Rock Creek Park, *P. occidentalis*, 16 Jun. 1895, M. B. Waite (BPI 611711); *P. occidentalis*, 1907, C. L. Shear (BPI 611747); *ibidem*, 19 May 1908, C. L. Shear (BPI 611745); *ibidem*, 4 Jun. 1908, C. L. Shear C. L. (BPI 611746); *ibidem*, 25 May 1910, D. W. Stier (BPI 611721); Iowa: Ames, *P. occidentalis*, 2 Jun. 1927, (collector unknown) (BPI 611691); Maryland: Prince George's Co., College Park, *P. occidentalis*, 1952, W. F. Jeffers (BPI 611724); Prince George's Co., Beltsville, near B011A, *P. occidentalis*, 5 Jul. 2005, M. V. Sogonov MS0211 (BPI 871956); Massachusetts: Boston, *P. occidentalis*, 14 Jun. 1930, V. Schmitt (BPI 611732); Boston, Arnold Arboretum, *P. occidentalis*, 10 Jul. 1930, J.H. Faull (BPI 611730); New Jersey: Riverton, *P. occidentalis*, 23 May 1910, J. L. Lipincott (BPI 611726); New York: Brooklyn, *P. orientalis*, 16 Jun. 1897, L. Collins Lewis (BPI 611764); Brooklyn, Prospect Park, *P. orientalis*, 28 Jun. 1916, G. M. Reed (BPI 611756); Brooklyn?, Botanic Garden, *P. orientalis*, 19 Jun. 1916, G. M. Reed (BPI 611757); *ibidem*, 29 Jun. 1917, G. M. Reed (BPI 611759); Ithaca, *P. occidentalis*, Jul. 1916, V. Tapke (BPI 611749A-B); Ithaca Flats, *P. occidentalis*, 25 Oct. 1906, H. H. Whetzel (BPI 611736); *ibidem*, 25 Oct. 1906, H. H. Whetzel (BPI 611755); Long Island, Queens, *P. orientalis*, 22 Jun. 1916, G. M. Reed (BPI 611758); Pawling, *P. occidentalis*, 03 Jul. 1916, C. D. Howe (BPI 611708); Ohio: *P. occidentalis*, 08 Jul. 1927, E. W. Mendenhall (BPI 611737); Tennessee: Blount Co., Great Smoky Mountains National Park, Cades Cove, intersection of Parsons Branch & Forge Creek Roads, *Platanus occidentalis*, 24 May 2006, M. V. Sogonov MS0394 = AR 4310 = CBS 120398 (BPI 872190); Washington: Spokane Co., Spokane, *P. occidentalis*, 30 Jul. 1932, F. D. Heald (C.G. Shaw 2256 = BPI 611716); West Virginia: Mingo, *P. occidentalis*, 29 Aug. 1903, W. A. Kellerman (BPI 611713); Morgantown, *P. occidentalis*, 23 May 1912, (collector unknown) (BPI 611805); Wisconsin: Madison, *P. occidentalis*, 5 Oct. 1910, O. A. Reinking (BPI 611750).

Anamorph on overwintered leaves: Czech Republic: Bohemia, Turnov, *P. orientalis*, Mar. 1906, J. E. Kabat (BPI 393079, BPI 393080). — Germany: vicinity of Bad Schandau, Prossen, *P. acerifolia*, 30 Apr. 1908, W. Krieger (Sydow 837 = BPI 393075, BPI 393076). — USA: Maryland: Montgomery Co., Gaithersburg, Seneca Creek State Park, near Seneca Creek Road, mixed forest, *P. occidentalis*, 19 Feb. 2005, M. V. Sogonov MS0132 (BPI 871951, derived culture AR4199); Prince George's Co., Beltsville, USDA ARS, hardwood forest near intersection of Powder Mill Road and Edmonston Road, *P. occidentalis*, 6 Feb. 2005, M. V. Sogonov MS0115 (BPI 871949, derived culture CBS 119029 = AR 4192); Prince George's Co., Beltsville, USDA ARS, mixed forest near Building 011A, *P. occidentalis*, 11 Feb. 2005, M. V. Sogonov MS0122 (BPI 871950, derived culture AR4198); *ibidem*, *P. occidentalis*, 5 Mar. 2005, M. V. Sogonov MS0137 (BPI 871952); *ibidem*, *P. occidentalis*, 7 Apr. 2005, M.V. Sogonov MS0168a (BPI 871944A, derived culture AR4163).

Additional cultures examined: France: Biarritz, *Platanus acerifolia*, 20 Jun. 1986, H.A. van der Aa 9828 (CBS 342.86). — Germany: *Platanus* sp., H. Zycha (DSM 62551 = IMB 12479); *Tilia cordata*, H. Butin G214 (DSM 4997). — New Zealand: Mid Canterbury,

Christchurch, *P. orientalis*, isol. 1 Mar. 1978, L. Hitchcock (ICMP 6201, ICMP 6202, ICMP 6203).

Notes: Although *Hymenula platani* Lév. 1848 provides the earliest epithet for the anamorph species in *Discula*, the name is already used by *Discula platani* Sacc., 1884.

Apiognomonia errabunda (Roberge ex Desm.) Höhn., Ann. Mycol. 16: 51 (1918). (Fig 2A–N)

Basionym: *Sphaeria errabunda* Roberge ex Desm., Ann. Sci. nat., Bot., ser. 3 10: 355 (1849).

Gnomonia errabunda (Roberge ex Desm.) Auersw. in Gonnerm. & Rabenhorst. Mycol. Eur. 5/6, p. 25 (1869).

Types: France: on dry leaves of *Fagus sylvatica*, spring, 1849, M. R. Roberge, Plantes Cryptogames de France 1791 (BPI bound — *lectotypus hic designatus*). — Switzerland: Vaud, Chexbres, La Cornallaz, on overwintered leaves of *Fagus sylvatica*, 8 May 1989, M. Monod 422 (LAU, derived culture CBS 775.79 — *epitypus hic designatus*).

Laestadia errabunda f. *tiliae* Rehm, Hedwigia 41: 203 (1902).

Apignomonia tiliae (Rehm) Höhn., Hedwigia 62: 48 (1920).

Type: Germany: Saxony, Königstein-an-der-Elbe, on overwintered leaves of *Tilia ulmifolia*, 6 May 1899, W. Krieger, Fungi Saxonici 1473 (BPI 611390 — *lectotype designated herein*, also as BPI bound and Rehm, Ascomyceten 1426 FH).

Gnomonia quercina Kleb., Haupt- u. Nebenfr. Askom.: 178 (1918).

Type: Germany: Niendorf, near Hamburg, on *Quercus robur*, August 1906, Iconotype p. 184–185 (BPI).

Gnomonia tiliae Kleb., Haupt- u. Nebenfr. Askom.: 202 (1918).

Type: Germany: Triglitz, on leaves of *Tilia cordata* (Iconotype p. 204 at BPI — *lectotypus hic designatus*).

Synonyms of the *Discula* anamorph of *Apiognomonia errabunda*: *Gloeosporium tiliae* Oudem., Nederl. kruidkund. Arch., ser. 2 1: 260 (1873).

Myxosporina tiliae (Oudem.) Höhn., Hedwigia 62: 48 (1921).

Gloeosporidium tiliae (Oudem.) Petr., Ann. mycol. 20: 15 (1922).

Types: The Netherlands: Zuidwijk near Naaldwijk, on living leaves of *Tilia cordata*, date unknown, J. E. van der Trappen (L 0194371 — *lectotypus hic designatus*). — Switzerland: Vaud, Le Mormont, Eclépens, *Tilia cordata*, 24 May 2005, M. Monod MS0189 (BPI 871958 *epitypus hic designatus*, derived culture CBS 119037 = AR 4179).

Labrella fagi Roberge, in Desmazières, Ann. Sci. nat. Bot., sér. 3 20: 225 (1853).

Gloeosporium fagi (Roberge) Westend., Bull. Acad. Roy. Belg., sér. 2 11: 313 (1861).

Gloeosporidium fagi (Roberge) Höhn., Sber. Akad. Wiss. Wien, Math.-naturw. Kl., Abt. 1 125: 95 (1916).

Myxosporina fagi (Roberge) Höhn., Hedwigia 62: 48 (1921).

Type: France: Normandy, in foliis languescentibus vel exsiccatis *Fagi*, autumn 1849?, J.B.H.J. Desmazières, Plantes

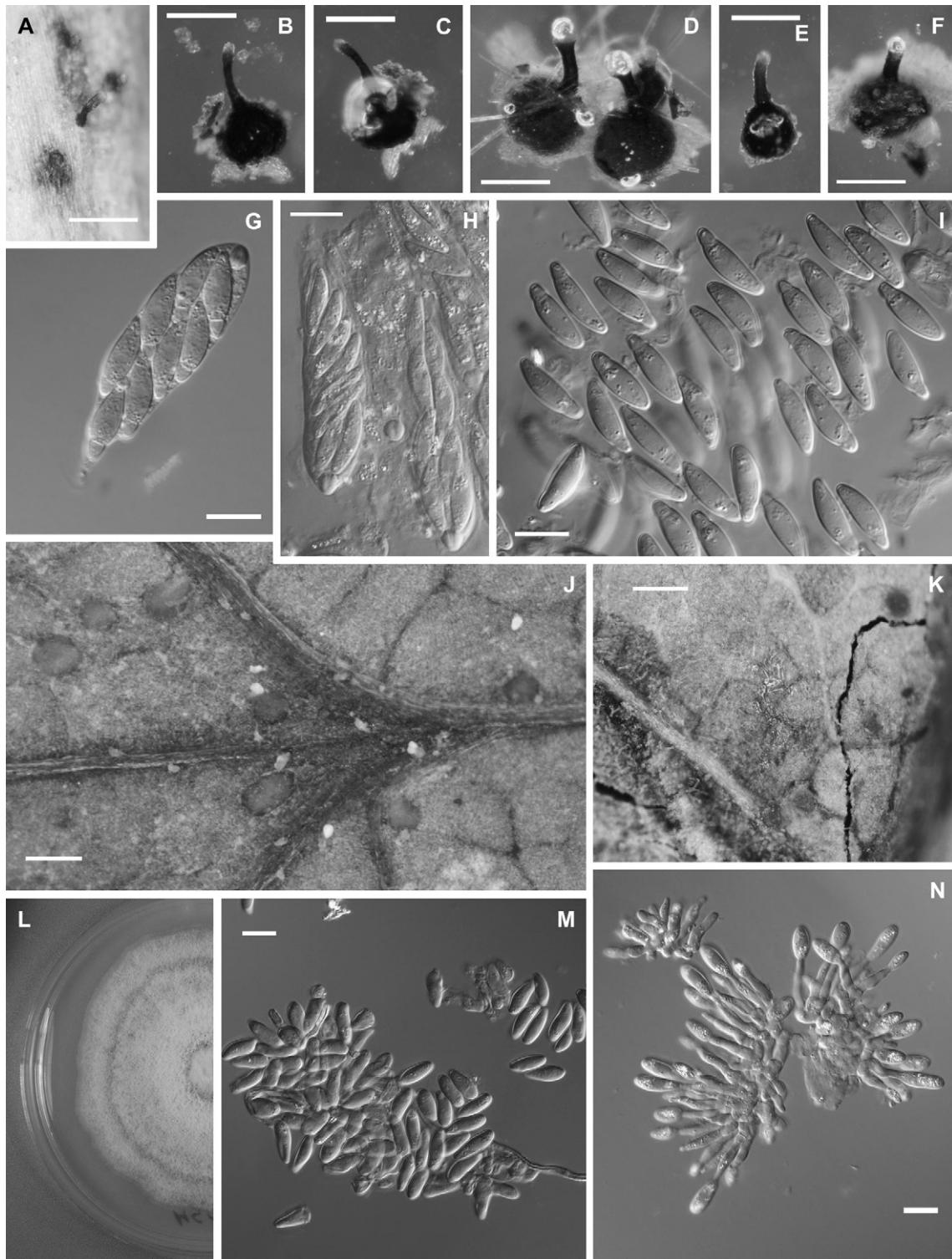


Fig 2 – *Apiognomonia errabunda* teleomorph and anamorph states. (A) Perithecium on a leaf. (B–F) Extracted and rehydrated perithecia showing variability in length and placement of beak. (G, H) Ascii. (I) Ascospores. (J, K) Acervulae on leaves. (L) Colony on PDA after 12 d of cultivation. (M) Conidia from acervulae on leaves. (N) Conidiophores and conidia from acervulae on leaves. Specimen (culture) numbers: (A, E) Monod 76. (B, C) Monod 506 (CBS 777.79). (D) Monod 468 (CBS 776.79). (F) Monod 94. (G, L) BPI 871943 (CBS 119037). (H) Monod 422 (CBS 775.79). (I) BPI 611383. (J) BPI 871958 (CBS 119037). (K) BPI 396105. (M) BPI 611781. (N) BPI 395103. Host plants: (A, E, G–I, L) *Fagus sylvatica*. (B, C) *Populus tremula*. (D) *Epilobium angustifolium*. (F) *Quercus robur*. (J) *Tilia cordata*. (K) (M) *Q. alba*. (N) *Q. pubescens*. Bars: (A–F, J, K) = 200 µm, (G–I, M, N) = 10 µm.

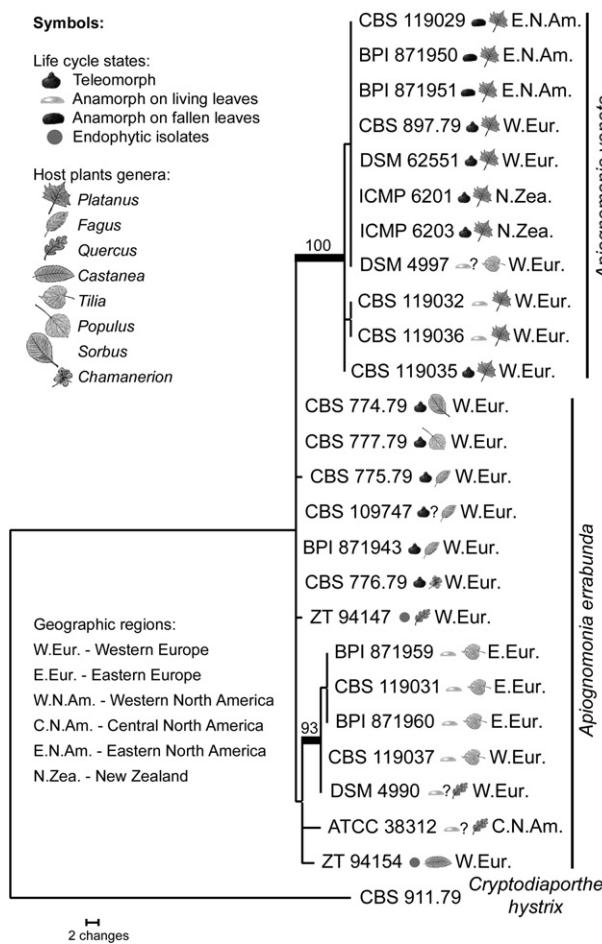


Fig 3 – One of 12 equally parsimonious trees obtained from analysis of combined dataset ITS1–5.8S–ITS2 rDNA and partial sequences of actin, calmodulin, and EF1- α using PAUP. Tree branches supported by 70 % or higher percentages based on 1K BS replications are given as thickened lines with their BS values indicated.

Cryptogames de France, ser. II, no. 77 (BPI bound – lectotypus hic designatus).

Fusarium nervisequum f. *quercus* Fuckel, Jarhb. nass. ver. Naturk. 23/24: 369 (1870).

Type: Germany: Hessen, Östricher Wald, living leaves of *Quercus*, summer 1869?, L. Fuckel [Fungi Rhenani 428 (BPI bound) – lectotypus hic designatus].

Gloeosporium exsiccans Thüm., Öst. Bot. Zeitschr. 27: 271 (1877).

Type: Austria: Görz, on living leaves of *Fagus sylvatica* var. *atropurpurea*, spring, 1876, G. Bolle. Not seen.

Gloeosporium quernum Harkn., Bull. California Acad. Sci. 1: 33 (1884)

Type: USA: California: San Francisco, Golden Gate Park, on leaves and young shoots of *Quercus agrifolia*, Jun. 1882, H. W. Harkness (BPI 395509 – lectotypus hic designatus).

Gloeosporium fuckelii Sacc., Syll. Fung. 3: 713 (1884).
[*Gloeosporium fagi* Fuckel, Jarhb. nass. Ver. Naturk. 25/26: 53(341) (1871) non *Gloeosporium fagi* (Roberge) Westend. (1861).]

Type: Germany: Hessen, Östricher Hinterwald, on living leaves of *Fagus sylvatica*, summer 1894, L. Fuckel, Fungi rhenani 2303 (BPI 394756 – lectotypus hic designatus).

Gloeosporium fagicola Pass., in Passerin & Brunaud, Rev. Mycol. 8: 206 (1886)

Type: France: Charente-Inférieure, Saintes, on leaves of *Fagus sylvatica*. Not seen.

Gloeosporium canadense Ellis & Everh., J. Mycol. 5: 153 (1889).

Type: Canada: Ontario: London, Strathroy, on living leaves of *Quercus alba*, Jul. 1889, J. Dearness (North American Fungi 2782 BPI 394189 – lectotypus hic designatus).

Discula fagi Oudem., Nederl. kruidkund. Arch., ser. 2 5: 505 (1889).

Type: The Netherlands: The Hague, Haagsche Bosch, on twigs of *Fagus sylvatica*, 21 Sept. 1888, C. E. Destree (L bound – lectotypus hic designatus).

Gloeosporium tiliaecolum Allesch., Ber. Bayer. bot. Ges. 5: 20 (1897).

Type: Germany: Langheim, *Tilia cordata*, Aug. 1895, F. Rohnfelder (M 0100091 – lectotypus hic designatus).

Gloeosporium nervicolum C. Massal., Malpighia 17: 421 (1903).

Type: Italy: Prov. Verona, mt. Gadà near Trignago, on leaves of *Quercus pubescens*, Jun. 1903, C. Massalongo (BPI 395103 – lectotypus hic designatus).

Gloeosporium cecidophilum Trotter, Ann. mycol. 3: 524 (1905).

Type: Italy: Bosco Fontana near Mantova, on undersurface of leaves of *Quercus pedunculata*, Jun 1901; also on leaves of *Quercus sessiliflora*, June 1901. Not seen.

Gloeosporium divergens Peck, N.Y. State Mus. Bull. 150: 31 (1910).

Type: USA: New York: Albany Co., Menands, Jul. 1910, on living leaves of *Quercus alba*, C. H. Peck (NYS f 1029 – lectotypus hic designatus).

Gloeosporium marginans Bubák & Syd., Ann. Mycol. 13: 8 (1915).

Type: Germany: Schleswig-Holstein, Sylt, Lorsenhain, near Westerland, on leaves of *Quercus pendiculata*, Aug. 1911, H. Sydow (BPI 395036 – lectotypus hic designatus).

Morphological characteristics similar to those of *A. veneta* except as noted. Perithecial diam \times height = (132–)181–248 (–456) \times (90.5–)139–190(–349) μm (mean = 217 \times 167, s.d. 57.2, 46.9, $n_1 = 41$, $n_2 = 39$). Beak length (50–)113–184(–544) μm

(mean = 154, s.d. 86.2, n = 37), basal diameter (31.5–)39.5–53 (–66.5) μm (mean = 47.9, s.d. 9.66, n = 37), distal diameter (28.5–)42.5–53(–81) μm (mean = 48.2, s.d. 10.5, n = 37). Ascus length \times width = (41–)47.5–53.5(–64.5) \times (8.5–)11–15.5(–18.5) μm (mean = 50.6 \times 13.2, s.d. 4.8, 2.5, n₁ = 47, n₂ = 47), apical ring 2.5–4.5 μm diam. Ascospores (10.5–)15–16.5(–19.5) \times (3.5–)4.5–5.5(–6.5) μm (mean = 15.7 \times 4.8, s.d. 1.3, 0.6, n₁ = 304, n₂ = 304), 1:b (2.5–)3–3.5(–5) (mean = 3.3, s.d. 0.3, n = 304), septum at (10.5–)18.5–22(–35.5) % (mean = 20.3, s.d. 2.9, n = 302) of ascospore length from basal end.

Conidiomata on overwintered leaves are not known. Conidiogenous cells in conidiomata on living leaves and twigs (5.5–)10.5–14.5(–21.5) \times (2.5–)3.5–4.5(–6) μm (mean = 12.7 \times 3.8, s.d. 2.9, 0.6, n₁ = 172, n₂ = 172), 1:b (1.5–)2.5–4(–6.5) μm (mean = 3.4, s.d. 0.9, n = 172). Conidia (5–)10.5–12.5(–17.5) \times (2.5–)4.5–5.5(–10) μm (mean = 11.7 \times 5, s.d. 1.6, 0.72, n₁ = 1340, n₂ = 1340), 1:b (1.5–)2–2.5(–4.5) (mean = 2.4, s.d. 0.4, n = 1340).

Colonies after 14 d morphology variable. PDA: 27–35 mm, plane, velutinous to felty, orange white (5A2) to light orange (6A4), greyish orange (4B4–6B6) and brownish orange (6C4). Reverse greyish orange (5B5) to light brown (6D4) in centre to pale at margins. Margins even, low or subsurficial, neat. MEA: Colonies mostly 10–25 mm diam, plane to slightly convex, velutinous, glabrous, whitish, brownish orange (5C5) to brownish gray (6C3) in centre, orange white (5A2) to pale orange (5A3) at margins, sometimes slightly radially wrinkled. Reverse brownish orange (6C5) to light brown (6D4) in the centre, then greyish orange (5B5), at margins pale orange (5A3) or colourless. Occasionally colonies fast growing, filling 90 mm Petri dish in 14 d, whitish, cottony with colourless reverse. On both media, cultures, even freshly isolated, usually do not produce black, non-ostiolate pycnidia-like conidiomata. In this study, they only were observed in the culture CBS 120404 = AR 4293.

Hosts: Primarily on *Fagus*, *Quercus* and *Tilia*, occasionally on *Acer*, *Castanea*, *Chamerion*, *Populus*, *Rhus*, and *Sorbus*. The teleomorph occurs on overwintered leaves while the anamorph sporulates primarily on living leaves, rarely on twigs.

Geographical distribution: Common in temperate regions in the northern hemisphere including Canada (British Columbia, Ontario), Czech Republic, France, Georgia, Germany, Italy, the Netherlands, Russia (Novgorod, Nizhniy Novgorod, Tver' provinces), Sweden, Switzerland, UK, USA (California, Connecticut, Indiana, Iowa, Maryland, Massachusetts, New Jersey, New York, Oregon, Pennsylvania, Rhode Island, Washington, West Virginia, Wisconsin).

Specimens examined:

Teleomorphs: **Canada:** British Columbia: Vancouver, Stanley Park, *Quercus* sp., 12 May 2006, M. V. Sogonov MS0396 (BPI 872192, derived culture CBS 120400 = AR 4312). — **Czech Republic:** Roblin, Bohemia, Turnov, *Fagus sylvatica*, 2 May 1907, J. E. Kabat (BPI 611386); Bohemia, Turnov, *F. sylvatica*, 18 May 1907, K. J. Kabat (BPI 611384). — **France:** Normandy, Parc de Lebisey, near Caen, *Fagus* sp., Dec. 1842, M.R. Roberge (BPI 611381). — **Georgia:** Tbilissi prov., Bakurani, *F. orientalis*, 13 Jul. 1916, N. Woronichin (BPI 394757). — **Germany:** Brandenburg, between Sophienstadt and Grafenbrück, *F. sylvatica*, 22 Oct. 1914, P. Sydow (BPI 394762). — **Italy:** Parma, *T. platyphylla*, May 1877, G. Passerini [Thümen, *Mycotheca Universalis* 882 (BPI bound)]; Verona, Valle dei Tessari, near Cogolo, *Q. pubescens*, Sep. 1904, C. Massalongo (BPI 395104). — **Russia:** Nizhniy Novgorod province, Pil'na, ploshchad' Revolyutsii, *T. cordata*, 17 Jun. 2005, M. V. Sogonov MS0214 (BPI 871959); Novgorod province, Kholm, naberezhnaya reki Lovat', *T. cordata*, 10 Jun. 2005, M. V. Sogonov MS0215 (BPI 871960, derived culture AR 4223); Novgorod province, Kholm, town park, *T. cordata*, 7 Jun. 2005, M. V. Sogonov MS0217 (BPI 871962, derived culture AR 4220); Novgorod province, Kholm, ul. Spartakovskaya, *T. cordata*, 10 Jun. 2005, M. V. Sogonov MS0216 (BPI 871961, derived culture CBS 119031 = AR 4219) — **Sweden:** Uppland: Dalby parish, 'Jerusalem', *F. sylvatica*, 18 May 1978, 1348a (BPI 806002). — **USA:** Connecticut: Durham, *Q. alba*, 7 Jun. 1920, W. Filley (BPI 611788);

611374); *Q. robur*, 4 Apr. 1862, B. Auerswald (B); Brandenburg, *F. sylvatica*, 3 Apr. 1914, W. B. (BPI 611385). — **Russia:** Tver' province, Toropets district, Kosilovo, *Q. robur*, 6 Jun. 2005, M. V. Sogonov MS0280 (BPI 871160), Novgorod province, Kholm, valley of Kun'ya river, *Q. robur*, 9 Jun. 2005, D.N. Borisov MS0496 (BPI 872212). — **Switzerland:** Vaud, campground Rolle, *F. sylvatica*, 14 May 1976, M. Monod 58 (LAU); Vaud, Servion, *F. sylvatica*, 26 May 1976, M. Monod 74 (LAU); ibidem, *Q. robur*, 26 May 1976, M. Monod 76 (LAU); Vaud, Chexbres, La Cornallaz, *F. sylvatica*, 26 May 1976, M. Monod 85 (LAU); ibidem, *Q. robur*, 26 May 1976, M. Monod 86 (LAU); Vaud, forest uphill from Muraz (between Apples and l'Isle), *Q. robur*, 4 Jun. 1976, M. Monod 94 (LAU); ibidem, *F. sylvatica*, 4 Jun. 1976, M. Monod 95 (LAU); Vaud, Prilly, La Fleur-de-Lys, *F. sylvatica*, 22 Apr. 1977, M. Monod 217 (LAU); Vaud, Montreux, Gorges du Chauderon, *Sorbus aria*, 28 Apr. 1978, M. Monod 401 (LAU); Vaud, Chexbres, La Cornallaz, *Sorbus aria*, 08 May 1978, M. Monod 420 (LAU, derived culture CBS 774.79); Valais, between Gueroz and La Taillaz, *Epilobium angustifolium*, 20 Jun. 1978, M. Monod 468 (LAU, derived culture CBS 776.79); ibidem, *Populus tremula*, 24 Apr. 1979, M. Monod 506 (LAU, derived culture CBS 777.79); Vaud, Jouxtens, *Acer platanoides*, 8 May 1978, M. Monod 609 (LAU); Neuchâtel, Creux-du-Van, *F. sylvatica*, 9 Jun. 1978, M. Monod 630 (LAU); Vaud, Col du Mollendruz, *F. sylvatica*, 25 May 2005, M. Monod & M. V. Sogonov MS0195 (BPI 871943, derived culture AR 4185 = CBS 119109). — **United Kingdom:** Batheaston, *Fagus* sp., (date unknown), C.E. Broome (BPI 611383). — **USA:** Maryland: Prince George's Co., Beltsville, 5229 Cochran Rd, back yard, *Q. palustris*, 15 Feb. 2005, M. V. Sogonov MS0128 (BPI 871941); New York: Ithaca, *Q. alba*, 17 May 1907, C. W. Edgerton 2768 (BPI 611792).

Anamorph on twigs: **The Netherlands:** the Hague, Haagsche Bosch (Le Bois de la Haye), *F. sylvatica*, 21 Sep. 1888, C.E. Destree, (L 0194366 K. Holm & L. Holm lectotype of *Discella fagi*); Scheveningen, *Q. robur*, Dec. 1888, C. E. Destree (BPI 797850, together with the type of *Fusicoccum quercuum* Oudem.).

Anamorph on living leaves: **Canada:** London, *Q. bicolor*, (date unknown), J. Dearness (BPI 611797); Vineland, *Q. alba*, 25 Aug. 1931, D.L. Bailey (BPI 611793). — **Czech Republic:** Bohemia, Rovensko, *F. sylvatica*, 8 Oct. 1898, F. Bubák (BPI 394761).

— **France:** Normandy, Parc de Lebisey, near Caen, *Fagus* sp., Dec. 1842, M.R. Roberge (BPI 611381). — **Georgia:** Tbilissi prov., Bakurani, *F. orientalis*, 13 Jul. 1916, N. Woronichin (BPI 394757). — **Germany:** Brandenburg, between Sophienstadt and Grafenbrück, *F. sylvatica*, 22 Oct. 1914, P. Sydow (BPI 394762). — **Italy:** Parma, *T. platyphylla*, May 1877, G. Passerini [Thümen, *Mycotheca Universalis* 882 (BPI bound)]; Verona, Valle dei Tessari, near Cogolo, *Q. pubescens*, Sep. 1904, C. Massalongo (BPI 395104). — **Russia:** Nizhniy Novgorod province, Pil'na, ploshchad' Revolyutsii, *T. cordata*, 17 Jun. 2005, M. V. Sogonov MS0214 (BPI 871959); Novgorod province, Kholm, naberezhnaya reki Lovat', *T. cordata*, 10 Jun. 2005, M. V. Sogonov MS0215 (BPI 871960, derived culture AR 4223); Novgorod province, Kholm, town park, *T. cordata*, 7 Jun. 2005, M. V. Sogonov MS0217 (BPI 871962, derived culture AR 4220); Novgorod province, Kholm, ul. Spartakovskaya, *T. cordata*, 10 Jun. 2005, M. V. Sogonov MS0216 (BPI 871961, derived culture CBS 119031 = AR 4219) — **Sweden:** Uppland: Dalby parish, 'Jerusalem', *F. sylvatica*, 18 May 1978, 1348a (BPI 806002). — **USA:** Connecticut: Durham, *Q. alba*, 7 Jun. 1920, W. Filley (BPI 611788);

Indiana: Vincennes, *Q. alba*, 2 Jun. 1933, L. Pierce (BPI 611785); *Iowa*: near Boone, *Q. sp.*, 8 Jun. 1927, W. A. Archer? (BPI 611771); Iowa City, *Q. alba*, 23 May 1930, G. W. Martin (BPI 611780, BPI 611786); *Maryland*: Baltimore, *Q. alba*, 16 Jun. 1927, J. G. D. Paul (BPI 611773); vicinity of Baltimore, *Q. alba*, 18 Jun. 1927, G. G. Hedgecock (BPI 611775); *Massachusetts*: Boston, *Q. alba*, 10 Jun. 1930, R. D. Lowden (BPI 611777); Bridgewater, *Q. alba*, 22 Jun. 1910, A. B. Seymour (BPI 611783); Jamaica Plain, Arnold Arboretum, *Q. alba*, 9 Jun. 1931, G. D. Darker 3472 (BPI 611787); Lincoln, *Q. alba*, 20 Jun. 1930, J. de Normandie (BPI 611795); Newburyport, *Q. alba*, 11 Jun. 1938, G. O. Clark (BPI 611781); Weston, E. Campbell Estate, *Q. alba*, 3 Jun. 1930, E.W. Thompson (BPI 611778); *New Jersey*: New Brunswick, *Quercus* sp., Jul. 1890, B. D. Halsted (BPI 611767); *New York*: Ithaca, *Quercus* sp., Jun. 1916, V. F. Tapke (BPI 611770); Ithaca, Forest Home, *Q. alba*, [date unknown], W. H. Rankin (BPI 611791); Varna, *Q. alba*, 30 Jun. 1906, Edgerton 1094 (BPI 611794, BPI 611796); *Oregon*: Medford, *Q. kelloggii*, Jul. 1935, S. M. Zeller (BPI 611799); *Pennsylvania*: near York, *Q. alba*, 22 May 1954, A. G. Johnson (BPI 611784); *Rhode Island*: Providence, *Q. alba*, 23 Jul. 1930, P. Allen (BPI 611776); *Washington*: Okanogan Co., Alta Lake State Park, campground, *Rhus glabra*, 15 May 2006, M.V. Sogonov MS0375 (BPI 872189, derived culture CBS 120404 = AR 4293); *West Virginia*: Coopers Rock, Entrance road, *Q. alba*, 13 Jul 1955, [collector unknown] (BPI 611779); *Wisconsin*: Racine Co., Racine, *Q. alba*, Jul. 1890, J. J. Davis (North American Fungi 2673)

Additional cultures examined: **Germany**: *Quercus robur*, H. Butin G248 (DSM 4990). —**Switzerland**: Vaud, Aiguilles de Baulmes, Pies de St. Croix, *Fagus sylvatica*, teleomorph?, 28 May 1989, M. Monod S. Redlin AERR4 (AR 2813 = CBS 109747). — **USA**: *Wisconsin*: *Q. alba*, 1967, D. Neeley 89 (ATCC 38312)

Additional non-living cultures sequenced: **Switzerland**: Zug, Walchwil, *Q. robur*, endophytic isolate, Oct. 1993, G. Horat 324 (ZT 94147); ibidem, *Castanea sativa*, endophytic isolate, Oct. 1993, G. Horat 115 (ZT 94154).

Notes: Although *Labrella fagi* Roberge 1853 provides the earliest epithet for the anamorph species in *Discula*, the name is already used by *Discula fagi* Oudem. 1877.

Rejected names: All the synonyms of the anamorph of *Gnomonia errabunda* listed by von Arx (1963, 1970) were evaluated and some were determined not to be this anamorph based on the type specimen, protologue or both:

Gloeosporium quercinum Westend., Bull. Acad. Roy. Belg. 21: 233 (1854).
Myxosporina quercina (Westend.) Höhn., Hedwigia 62: 48 (1921).

Type: **Belgium**: Kortrijk, on senescent leaves of *Quercus* sp., (no date), M. van den Peereboom-Delacroix, Herbier Cryptogamic Belge 981 (FH bound).

The type specimen has much smaller conidia than those of *A. veneta* and *A. errabunda*. Conidia of the type species of *G. quercinum* were determined to be (5–)5.5–6.5(–7.5) × (2–)2.5–3(–3.5) µm (mean = 6.2 × 2.6, s.d. 0.7, 0.4, n₁ = 18, n₂ = 18), l:b (1.5–)2–2.5(–3) (mean = 2.42, s.d. 0.36, n = 18).

Gloeosporium umbrinellum Berk. & Broome, Ann. Magaz. nat.

Hist. 3 ser. 18: 7 (1866).

Gloeosporidium umbrinellum (Berk. & Broome) Petr. Ann. Mycol. 20: 15 (1922).

Discula umbrinella (Berk. & Broome) Morelet, Bull. Soc. Sci. nat. d'Arch. Toulon Var 203: 12 (1973).

Type: **United Kingdom**: Somerset: near Batheaston, Charmy Down, on fallen leaves of *Quercus*, Oct. 1865, M. J. Berkeley & C. E. Broome (K 130655).

The type specimen has longer and more slender conidia with straighter and less branched conidiophores and more yellow shades of acervulae than those of *A. veneta* and *A. errabunda*. Conidia of the type species of *G. umbrinellum* were determined to be (11.5–)12.5–14(–15) × (3.5–)4.5–5(–5.5) µm (mean = 13.4 × 4.6, s.d. 0.8, 0.4, n₁ = 40, n₂ = 40), l:b (2–)2.5–3(–3.5) (mean = 2.91, s.d. 0.26, n = 40). This name has been misapplied by Sutton (1980).

Discula quercina Cooke, Grevillea 12: 23 (1883).

Discula quercina (Cooke) Sacc., Syll. Fung. 3: 675 (1884).

Type: **USA**: South Carolina: Aiken, on bark of *Quercus nigra*, no date, H. W. Ravenel 2857 (Fungi Americani Exsiccati 555 = BPI 393265).

The description of *Discula quercina* in conidial dimensions given as 15 × 4 µm agrees with the concept of anamorphic *A. veneta* and *A. errabunda*. However, based on the isotype specimen examined, the conidia of *Discula quercina* are morphologically distinct from those in the original description and are shorter than those of *A. veneta* and *A. errabunda*. The conidia of the isotype specimen of *Discula quercina* have thickened, pigmented walls and are (7.5–)9–10.5(–11.5) × (3.5–)4.5–5(–5.5) µm (mean = 9.8 × 4.8, s.d. 1.0, 0.4, n₁ = 66, n₂ = 66), l:b (1.5–)2–2.5(–3) (mean = 2.1, s.d. 0.2, n = 66).

Gloeosporium fraxineum Peck, New York State Mus. Rep. 35: 137 (1884).

Discula fraxinea (Peck) Redlin & Stack, Mycotaxon 32: 194 (1988).

Type: **USA**: New York: Albany, living leaves of *Fraxinus pubescens*, Jun. 1883?, C. H. Peck. Not seen.

The original description indicates that conidia of *G. fraxineum* are smaller than those of *A. veneta* and *A. errabunda*. They are described as 0.0002'–0.00025' × 0.00016' ≈ 5–6.4 × 4 µm). In addition the host of *G. fraxineum* is on living leaves of a host plant unusual for anamorphic *A. veneta* and *A. errabunda*. Redlin & Stack (1988) provide a description of the anamorph and its teleomorph, *Gnomoniella fraxini* Redlin & Stack.

Gloeosporium aridum Ellis & Holw., J. Mycol. 3: 21 (1887).

Type: **USA**: Wisconsin: Racine, on living leaves of *Fraxinus americana*, Jun. 1886, J. J. Davis. Not seen.

Conidia of *G. aridum* described as 5–8 × 2.5–3.5 µm are smaller than those of *A. veneta* and *A. errabunda*. In addition the host of *G. fraxineum* is on living leaves of a host plant unusual for *A. veneta* and *A. errabunda*. This name is considered a synonym of *Discula fraxinea* (Peck) Redlin & Stack according to Redlin & Stack (1988).

Gloeosporium irregularare Peck, New York State Mus. Rep. 42: 127 (1889).

Type: USA: New York: Albany Co., Menands, leaves of *Fraxinus americana*, Jun. 1888, C. H. Peck (BPI 394843).

Conidia of *G. irregulare* are described as $0.0003' - 0.0004' \times 0.00016' - 0.0002' \approx 7.5 - 10.5 \times 4 - 5 \mu\text{m}$, smaller than those of *A. veneta* and *A. errabunda*. Conidia of the type specimen were $(6.5 - 8 - 9 - 10) \times (3.5 - 4 - 4.5 - 5) \mu\text{m}$ (mean = 8.4×4.2 , s.d. 0.9, 0.34, $n_1 = 24$, $n_2 = 24$). In addition the host plant is not typical of *A. veneta* and *A. errabunda*.

Gloeosporium celtidis Ellis & Everh. Proc. Acad. nat. sci. Phil.: 82 (1891).

Type: Canada: Ontario: London, Sep. 1890, J. Dearnness 319, North American Fungi 2665 (BPI bound).

The type specimen of *G. celtidis* reveals conidia that are fusiform rather than the ellipsoid to oval conidia of *A. veneta* and *A. errabunda*. In addition, the host of *G. celtidis* is not typical of *A. veneta* and *A. errabunda*.

Gloeosporium vagans Syd., Ann. mycol. 10: 448 (1912).

Type: Poland: Gorzów Wielkopolski region, Witnica municipality, Dąbroszyn (at the time of the publication: Germany: Brandenburg), garden by the palace Tamsel, leaves of *Acer stricta*, P. Vogel, Sydow, Mycotheca Germanica 1135 (BPI).

The original description of *G. vagans* suggests more slender conidia, $7 - 10 \times 2.5 \mu\text{m}$, than those of *A. veneta* and *A. errabunda*. The type specimen examined fits the description. The conidial measurements were $(7 - 9 - 10.5 - 12.5) \times (2.5 - 2.5 - 3 - 3.5) \mu\text{m}$ (mean = 9.8×2.9 , s.d. 1.8, 0.3, $n_1 = 8$, $n_2 = 8$).

Gloeosporium boemicum Kabát & Bubák, Hedwigia 52: 359 (1912).

Type: Czech Republic: Bohemia, near Hruba Skala (Gross-skal), forester's house Bukovina, living senescent leaves of *Aesculus hippocastanum*, J. E. Kabát, Sep.-Oct. 1911, Kabát & Bubák, Fungi Imperfecti Exsiccati 734 (BPI 394106).

The original description of *G. boemicum* suggests conidia, $5 - 9 \times 2.5 - 4 \mu\text{m}$, that are narrower than those of *A. veneta* and *A. errabunda*. Conidia of the type specimen were somewhat longer than in the original description but narrower than those of *A. veneta* and *A. errabunda*. The conidia of the type specimen of *G. boemicum* were determined to be $(9.5 - 10.5 - 13 - 13.5) \times 3 - 3.5 - (4 - 4.5) \mu\text{m}$ (mean = 11.5×3.4 , s.d. 1.4, 0.4, $n_1 = 6$, $n_2 = 6$).

Discussion

Apiognomonia veneta and *A. errabunda* are two closely related species distinguished by point mutations in the nucleotide sequences of four presumably unlinked genes (Table 2). One substitution each in the actin and calmodulin gene fragments and four in EF1- α separate the isolates into two clades. These clades are correlated with a *Platanus* or non-*Platanus* host association. *A. veneta* is strongly associated with *Platanus* spp.

wheras *A. errabunda* is found mostly on *Fagaceae*, less commonly on *Tilia*, and occasionally on different unrelated host plant species such as *Acer*, *Chamerion*, *Populus*, *Rhus*, and *Sorbus*. The only strain in which there is no agreement between molecular data and host association is DSMZ 4997 from *Tilia*, but it is molecularly identical to a typical *Platanus* isolate. This may be explained as an unusual host similar to that found in other gnomoniaceous species with similarly strict host association. For example, *Gnomonia gnomon* typically occurs on *Corylus* but one specimen was collected on *Populus* (Monod 1983; Sogonov et al. 2005). *G. setacea* is normally associated with *Quercus* and *Fagus* but has been collected once on *Platanus* (Sogonov, unpublished, specimen BPI 872200, derived culture AR 4314). In both these cases the morphological identification of these specimens on an atypical host was supported by sequence data. Geography was not correlated with nucleotide substitutions in either species.

Morphologically, the two species differ in subtle morphological characteristics. Ascospores of *A. veneta* are slightly more tapered at the apices than those of *A. errabunda* (compare Figs 1H and 2I). This is most apparent in free ascospores from fresh specimens as opposed to those remaining in intact asci. This character is not reliable in dried specimens as a non-reversible deformation of the ascospores occurs after being dried and stored. *A. veneta* also differs from *A. errabunda* by more abundant production of conidiomata in fresh cultures (compare Figs 1P and 2L). This was emphasized as one of the main differentiating characters by Monod (1983) and confirmed in this study. In nature, only *A. veneta* produces sporonema-like conidiomata on fallen leaves in winter and early spring, although it is not known whether the sporonema-like state is an inherent character of the fungus or a response to an environmental influence. In general, specimens of *A. errabunda* have longer perithecial beaks as compared with *A. veneta* (Figs 1A-E and 2A-F) as observed here and by Monod (1983). However, the lower range of perithecial beak lengths in *A. errabunda* overlaps that of *A. veneta*. Using this suite of morphological characters, fresh collections of these two species can be readily distinguished. Based on these morphological observations and molecular data presented here, *A. errabunda* is considered to be distinct from *A. veneta*, thus, the correct name for the type species of *Apiognomonia* is *A. veneta*.

The anamorphic states of *Apiognomonia* generally have been recognized in *Discula*. As mentioned above, the lectotype species of *Discula* as designated by von Höhnel (1915) is *D. platani* Sacc. 1884. Type specimens of the numerous synonyms of *D. platani* were examined and it was determined that the correct name for the type species of *Discula* is *D. nervisequa*, the anamorph of *A. veneta*. The earliest name for the anamorph of *A. errabunda* is *Labrella fagi* Desm. & Roberge 1853. If placed in *Discula*, this name would be a later homonym of *Discula fagi* Oudem. 1899. Likewise, the name *Gloeosporium quercinum* West. 1854 would be a later homonym of *Discula quercina* (Cooke) Sacc. 1884. Based on von Arx (1970), the next available epithet is *G. umbrinellum* Berk. & Broome 1866. The type specimen of *G. umbrinellum* on *Quercus* was examined and determined to be something different than the anamorph of *A. errabunda*. This name has been erroneously applied to the anamorph of *A. errabunda*. The earliest epithet for the anamorph of *A. errabunda* is *G. tiliae* Oudem. 1873. However, rather than transfer this name to

Discula and introduce an unneeded name, *A. errabunda* is used to refer to the anamorph as well as the teleomorph.

Some confusion concerning the identity of a number of sequences in GenBank was revealed by a BLAST search (<http://www.ncbi.nlm.nih.gov/BLAST>) in GenBank performed with the ITS sequences of *A. veneta* and *A. errabunda*. Sequences with accession numbers AJ293872–AJ293875 and AY853206–AY853214 from strains isolated from *Quercus* and identified as *Fusicoccum quercus* were found to be identical or nearly so to those of *A. errabunda*. *F. quercus* is considered to be an anamorphic state of *Botryosphaeria* (*Botryosphaeriaceae*, *Dothideales*) (<http://www.indexfungorum.org/Names/namesrecord.asp?RecordId=180714>). In order to determine whether *F. quercus* is actually one of the numerous synonyms of the anamorphic state of *A. errabunda*, the original description (Oudemans 1889) and the type specimen of *F. quercus* (the Netherlands, Scheveningen, *Quercus robur*, Dec. 1888, C. E. Destree – BPI 797850) were examined. This specimen contains a single 3 cm long oak twig with two different fungi on it. One fungus corresponds to the *A. errabunda* anamorphic state whereas the other has black thick-walled conidiomata and longer and more slender conidia (10–12–13(–15.5) × (3–)3.5–4(–4.5) µm (mean = 12.7 × 3.7, s.d. 1.0, 0.3, n = 42), 1:b (2.5–)3–4(–5) (mean = 3.5, s.d. 0.4, n = 42). Since Oudemans (1889) described the stromata of *F. quercus* as ‘...nigra, ... intus distincte pluricellata’ with conidia measuring 14 × 3.5 µm, it was determined that the description and thus the binomial refer to the second fungus and not the anamorphic state of *A. errabunda*. Based on ITS sequences, we consider the identity of the strains corresponding to the sequences AJ293872–AJ293875 and AY853206–AY853214 to be *A. errabunda* and not *F. quercus*.

Neely & Himelick (1967) carried out a comparison of diverse morphological, cultural, physiological and phytopathological characteristics of isolates of *A. errabunda* from *Quercus alba* and *Platanus occidentalis*. The authors concluded that the isolates on *Quercus* were different from those on *Platanus* and should be recognized as two different species because of minor differences in ascii, ascospore and conidial sizes and shapes as well as differences in colony morphology on PDA and optimal growth temperature. In addition, isolates from *Quercus* did not infect *Platanus* and vice versa in greenhouse experiments. The authors reported a striking difference in the length of perithecial beaks between isolates on *Quercus* and those on *Platanus*. Long perithecial beaks such as those reported by Neely & Himelick (1967) have not been reported for *A. errabunda* and were not observed in our study. We suggest that the fungus on *Quercus* with such long beaks might have been *Gnomonia setacea* (Pers.: Fr.) Ces. & De Not., a common inhabitant of over-wintered oak leaves (Sogonov et al. 2005). Unfortunately, no specimens or cultures from that study were deposited in herbaria or culture collections and thus it is impossible to know what actual species were studied.

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